Limnologica 33, 122–130 (2003)
© Urban & Fischer Verlag
http://www.urbanfischer.de/journals/limno

LIMNOLOGICA

Effects of inter- and intraspecific competition on growth and development of *Bufo viridis* and *Bufo bufo* tadpoles

Sophie Katzmann, Andrea Waringer-Löschenkohl*, Johann A. Waringer

Institute of Ecology and Conservation Biology, University of Vienna, Austria

Received February 14, 2003 · Accepted March 6, 2003

Abstract

Competition between the common toad *Bufo bufo* (L.) and the green toad *Bufo viridis* LAURENTI was studied in an experimental design. Mixed and single-species groups of 40 larvae were reared in plastic tanks (water volume 41 l). Growth parameters such as body length, total length, body mass and developmental stage according to GOSNER (1960) were measured weekly until metamorphic climax and analyzed by regression analysis. Body condition index was calculated. Tadpoles of *B. bufo* reached metamorphosis at the same time in mixed and single-species treatments. Larvae and toadlets were insignificantly larger in single-species groups, weighed more and had a higher body condition index than in mixed species designs. In *B. viridis* the larval period was six days shorter in mixed groups; tadpoles and toadlets were smaller but had a higher body condition index than in the single-species treatment. These results indicate high intraspecific competition in *B. viridis* and competitive inferiority of *B. bufo* to *B. viridis* under the experimental conditions.

Key words: *Bufo bufo* – *Bufo viridis* – tadpoles – competition – growth – development

Introduction

Competition in amphibian larvae has been a focus of research in laboratory experiments (e.g. WILBUR 1977; TRAVIS 1980) and artificial ponds (e.g. MORIN & JOHNSON 1988; WILBUR 1987; GRIFFITHS et al. 1993; WERNER 1994). Often strong asymmetric intra- and interspecific effects on growth rates and timing of metamorphosis due to exploitation and interference competition were revealed (MORIN & JOHNSON 1988; WERNER 1994; WERNER & ANHOLT 1996; BEEBEE 1995; PETRANKA 1995; BAKER & BEEBEE 1997; KUPFERBERG 1997; PEACOR & WERNER 1997; BARDSLEY & BEEBEE 1998b; KIESECKER & BLAUSTEIN 1999; SINSCH et al. 1999; LAURILA 2000; WONG et al. 2000). Amphibians breed in a variety of freshwater habitats ranging from extremely temporary to permanent ponds and optimize their fitness by a high plasticity in larval life history traits, especially when developing in unpredictable environments (WILBUR & COLLINS 1973; NEWMAN 1992; MERILÄ et al. 2000). In small temporary pools, tadpoles encounter fewer predators, profit from higher temperatures, but also suffer from a high desiccation risk. Consequently, larvae of temporary pond species tend to be more active and have higher growth and developmental rates (TEJEDO & REQUES 1994a,b; LOMAN 1999; MERILÄ et al. 2000) than species living in predator-rich permanent ponds (MORIN 1983; WOODWARD 1983; WELLBORN et al. 1996; LAURILA 1998). Many authors consider that they are the superior competitors and can have a negative effect on permanent pond species (WOODWARD 1982; WILBUR 1987).

***Corresponding author:** Dr. Andrea Waringer-Löschenkohl, Institute of Ecology and Conservation Biology, Althanstraße 14, A-1090 Vienna, Austria. e-mail: waringer@pflaphy.pph.univie.ac.at

In cultivated, agriculture-dominated landscapes, amphibian breeding sites have become rare, constraining species with different demands to share suboptimal habitats. Contrary to the expected superiority of temporary pond breeders, *Bufo calamita*, a species of pioneer habitats, turned out to be competitively inferior to the permanent pond species *Bufo bufo*, when forced to use the same habitats in deprived environments in England (BANKS & BEEBEE 1987).

In the Lower Austrian Weinviertel the situation is similiar: Two *Bufo* species with different life cycles and habitat demands share their breeding ponds (KATZMANN 2002), a situation which is rather rare (HEMMER & KADEL 1970; HEMMER & BOEHME 1974; SINSCH et al. 1999; CABELA et al. 2001). The green toad *Bufo viridis* is a species of open landscapes, which develops in temporary shallow pools, whereas the common toad *Bufo bufo* is a woodland species, typically spawning in large permanent ponds, often even together with fish (NÖLLERT & NÖLLERT 1992). *B. bufo* tadpoles are unpalatable to most vertebrate predators (HEUSSER 1971), they are very active swimmers and form shoals (EIBL-EIBESFELDT 1953; GRIFFITHS & FOSTER 1998). Whilst *B. bufo* is an early spring-explosive breeder, *B. viridis* has several spawning periods from spring to early summer (NÖLLERT & NÖLLERT 1992).

The aim of the present study was to examine whether syntopic larval development of the two species produces competitive effects manifested in modified growth, developmental rates or body condition. In order to exclude environmental effects and predation pressure, an experimental design in the laboratory was chosen.

Material and Methods

Breeding habitats

Spawn of *Bufo bufo* was collected from a small permanent forest pond used as a game watering place at Seyring (16°30′48″ E; 48°20′54″ N; 167 m sea level), approximately 22 km NNE of Vienna in the Weinviertel, Lower Austria. The pond is situated in a clearing close to the border of a deciduous forest. The groundwater-fed, circular waterbody is up to 8 m in diameter and up to 2.5 m deep. The bottom is covered by gravel and leaf litter. The riparian vegetation is well developed and consists of reed belts [*Phragmites australis* (CAV.) TRIN. ex STEUD.] and adjacent shrubs and brush. In addition, a shallow riparian zone exists in the SE corner. Until noon the water surface is completely insolated. From April to June, water temperatures ranged from 5 to 26 °C, pH from 6.90 to 8.52, conductivity from 783 to 785 µS cm^{-1} and oxygen concentration from 4.3 to 12.5 mg l^{-1}. Besides a rich invertebrate fauna, aquatic vertebrates observed at this site comprised *Cyprinus carpio* L., *Triturus vulgaris* L., *Rana dalmatina* BONAPARTE and *Natrix natrix* L.

Spawn of *B. viridis* was obtained from an artificial and rain-fed waterbody located in the fields at Obersdorf (16°32′14″ E; 48°22′28″N; 180m sea level), approximately 20 km NNE of Vienna in the Weinviertel, Lower Austria. The water is up to 6 m wide, roundish and up to 85 cm deep. Due to its dependency on precipitation, water level fluctuations are very high, and the waterbody dries up occasionally. The hinterland consists of fields, vineyards and hedges. As trees and bushes are completely lacking, insolation is high and lasts for the whole day. From April to July, water temperatures ranged from 6 to 29 °C, pH from 7.05 to 9.37, conductivity from 124 to 186 µS cm^{-1} and oxygen concentration from 13.1 to 17.1 mg l^{-1}. At this location, both *Bufo* species (*B. bufo*, *B. viridis*), along with *Rana dalmatina* and *Rana* kl. *esculenta* L. were observed. The fish fauna consisted of *Gobio gobio* L. only.

Experimental design

Spawn of *B. bufo* [developmental stages 4–5 following GOSNER (1960); Fig. 1] was collected from the pond at Seyring on March 25th 2001 and spawn of *B. viridis* was obtained from the waterbody in the fields at Obersdorf on April 3rd 2001, containing eggs in the same developmental stages as the former species.

In the laboratory the spawn was bred at 12–18 °C, following the temperature regime of the ponds outside. Tadpoles of *B. bufo* hatched on April 3rd, those of *B. viridis* on April 12th. In order to follow the phenological pattern of the species larvae were put into aerated plastic tanks (56.5 × 36.5 × 30.0 cm) as soon as they reached Gosner stage 25/26 (Fig. 1). So, similar to field conditions, *Bufo bufo* larvae were transferred into the tanks first and consequently reached metamorphosis before *B. viridis*. The tanks were filled with 41 l of tap water (pH = 7.4–7.55; conductivity = 200–222 µS cm^{-1}) two weeks prior to the start of the experiment.

To provide habitat structure each tank contained thin layers of field soil and stands of macrophytes (*Potamogeton lucens* L.). All tanks used in the experiment were placed next to each other and situated close to the window front in order to provide the same temperature and natural light conditions. During the experiments the temperature in all plastic tanks varied between 19 and 22 °C. Altogether nine experimental ponds were installed, containing three different groups with three replicates each: Three tanks contained 40 tadpoles of *B. bufo* each (*B. bufo* control), three tanks 40 larvae of *B. viridis* each (*B. viridis* control) and three tanks 20 tadpoles of *B. bufo* and 20 of *B. viridis* (mixed groups). At the beginning of the experiments all tadpoles were measured. Variables measured weekly were body length (snout to anus), total length (snout to tail end), developmental stage (GOSNER 1960) and body mass. The final

size at metamorphosis was measured at the end of the experiments in stage 45/46 (Fig. 1). Body mass was determined from developmental stage 33 (*B. bufo*) or stage 36 (*B. viridis*), because tadpoles were too small in earlier stages. Towel-dried wet mass of each tadpole was measured to the nearest 0.001 g. Dead larvae were removed from the tanks.

During the experiment, larvae were fed on a mixture of Tetramin fish food and dried nettles (*Urtica dioica* L.) three times a week. The ration was calculated as 0.1 g × mean tadpole mass per day per tadpole, following the procedure suggested by GRIFFITHS & FOSTER (1998). After termination of the experiments all toadlets were released at their original habitats.

Statistical Analysis

Statistical tests were performed using STATISTICA, Version 5.0, Statsoft Company. Differences in development between treatments (control and mixed groups) were analysed by Kruskal-Wallis tests. Slopes of regression lines of the control and the mixed groups were tested for significance following the procedure given by ZAR (1984).

Differentiation (developmental stages as a function of time) were well defined by a linear regression:

$$Y = a + b * x \quad (1)$$

whereas growth (body length and total length as a function of time) are given by the following asymptotic relationship:

$$Y = Y_{max} - a * e^{(-b * x)} \quad (2)$$

where Y_{max} is the highest Y value recorded.

The body condition index (b) was calculated following VIERTEL (1981):

$$\log b = \log \text{mass} - 3 * \log \text{total length} \quad (3)$$

All graphics were done with STATISTICA.

Results

Duration of the larval period, development

Tadpoles of *B. bufo* reached stage 25/26 (Fig. 1) on April 19th, those of *B. viridis* on May 2nd 2001. For *B. bufo* the mean duration of the larval period lasted 58 days and did not differ significantly ($p > 0.05$) between the control and the mixed groups. The relationship between time and developmental stage following GOSNER (1960) was well defined by a linear regression line (Fig. 2, Table 1). For *B. viridis* there were significant differences ($p < 0.001$) in the length of the larval period. Individuals of the control group needed 83 days to reach metamorphic climax, those of the mixed group needed only 77 days; this is shown in Fig. 2 by the higher slope

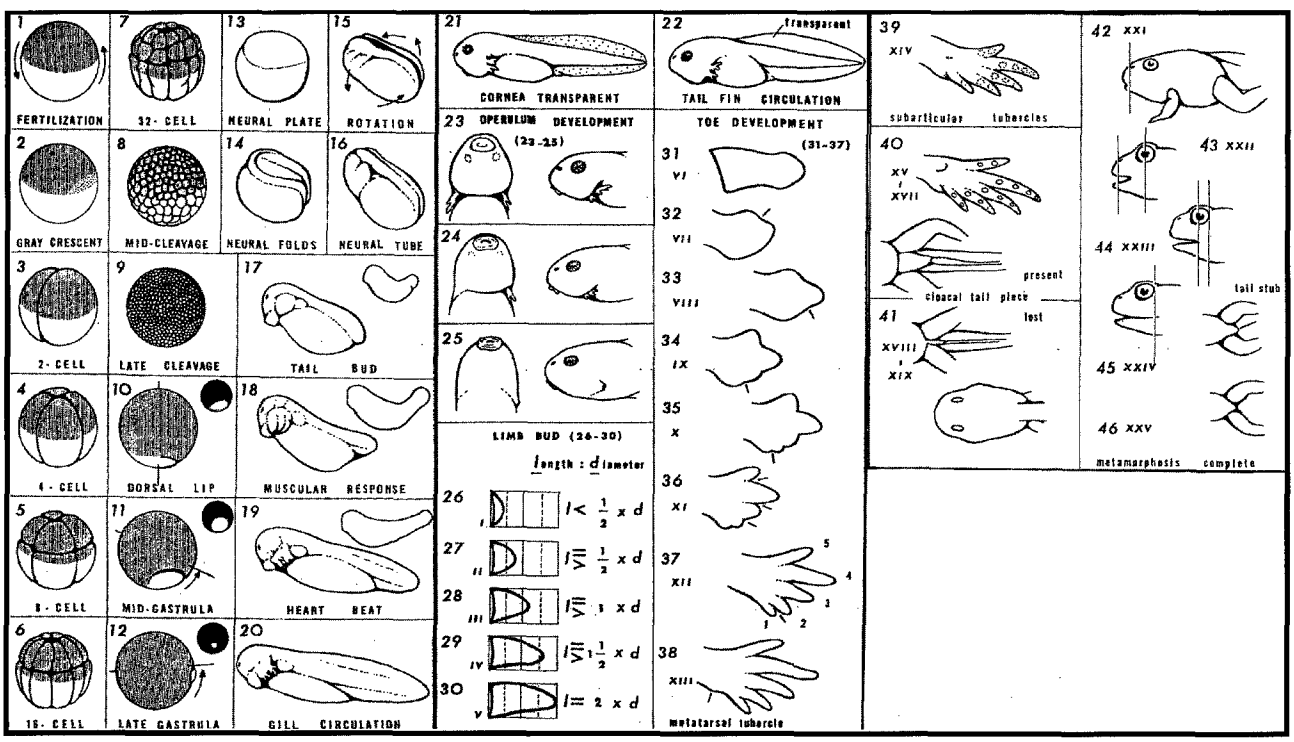

Fig. 1. Developmental stages of anuran embryos and larvae (after GOSNER 1960).

(= higher developmental rate) of *B. viridis* in mixed-group treatments. The difference between the slope of 0.32 (control) and 0.37 (mixed) was very highly significant (ZAR 1984; $p < 0.001$), showing that *B. viridis* had a shorter larval period in mixed groups, while there was no effect on *B. bufo*.

Growth

At the start of the experiments, larvae of *B. bufo* were larger than those of *B. viridis;* from larval developmental stage 35 (GOSNER 1960), however, *B. viridis* larvae became larger than those of *B. bufo* and maintained their

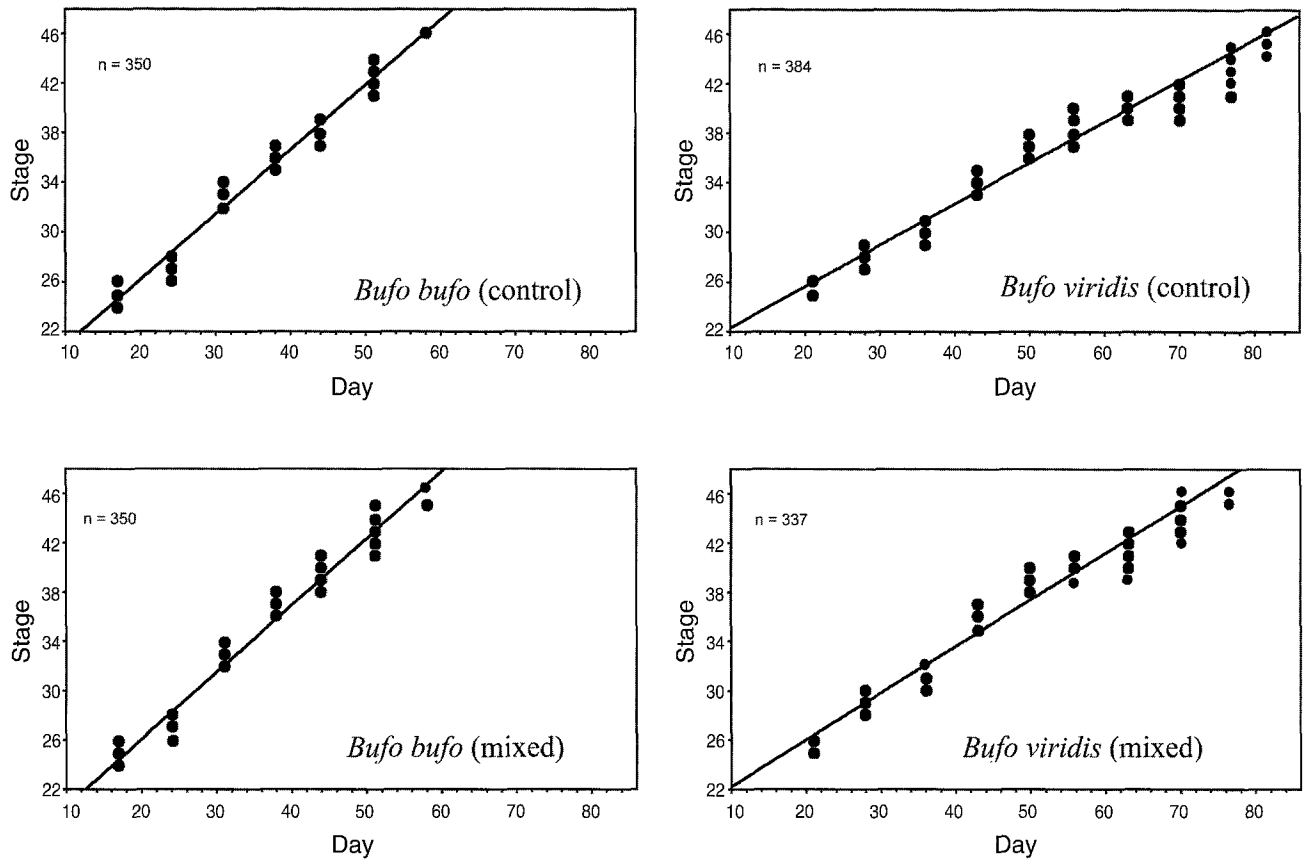

Fig. 2. Relationship between time (days) and larval developmental stage after GOSNER (1960) of *B. bufo* and *B. viridis* in control and mixed groups. Day 1 = hatching day (04 Apr 2001 for *B. bufo* and 12 Apr 2001 for *B. viridis*). Regression parameters are given in Table 1. Due to overlapping, each dot may represent numerous tadpoles.

Table 1. Regression parameters of the relationship between time (x; days) and larval developmental stage after GOSNER (1960) (y) of *B. bufo* and *B. viridis* in control and mixed groups; df = degrees of freedom, F = value of F statistic.

	r^2	df	F	Probability level
B. bufo control	0.98	348	21583	<0.001
B. bufo mixed	0.98	348	14178	<0.001
B. viridis control	0.96	382	12068	<0.001
B. viridis mixed	0.96	335	7914	<0.001

Regression equation:

B. bufo control:	$y = 15.79 + 0.52^* \times$
B. bufo mixed:	$y = 15.54 + 0.53^* \times$
B. viridis control:	$y = 19.64 + 0.32^* \times$
B. viridis mixed:	$y = 18.90 + 0.37^* \times$

Table 2. Regression parameters of the relationship between time (x; days) and body length (y; mm) of *B. bufo* and *B. viridis* in control and mixed groups; df = degrees of freedom, F = value of F statistic.

	r^2	df	Probability level
B. bufo control	0.94	348	<0.001
B. bufo mixed	0.94	345	<0.001
B. viridis control	0.96	382	<0.001
B. viridis mixed	0.98	335	<0.001

Regression equation:

B. bufo control:	$y = 13–30.72^* e^{(-0.07^* x)}$
B. bufo mixed:	$y = 13–27.38^* e^{(-0.06^* x)}$
B. viridis control:	$y = 20–36.81^* e^{(-0.03^* x)}$
B. viridis mixed:	$y = 18–43.34^* e^{(-0.05^* x)}$

size advantage until the end of the experiments. The relationships between time and body length were asymptotic for both species and both treatments (mixed, control; Fig. 3, Table 2). For both species body length increased in a linear pattern from developmental stage 25 until stage 38/39, after which it remained stationary. In addition, the total length increase of both species was linear until stage 40, after which larvae began to shorten their tail. *B. bufo* tadpoles were larger in control groups than in mixed groups, but the difference was not significant ($p > 0.05$). In all developmental stages *B. viridis* had larger tadpoles in mixed groups. The difference of the growth rates was highly significant ($p < 0.01$).

Information on larval developmental stages and body lengths of tadpoles co-occurring in mixed group treatments is given in Fig. 4.

Body mass, body condition

For both groups (control, mixed) of *B. bufo*, body mass increased until stage 37/38, but was significantly higher (Kruskal-Wallis ANOVA; $P < 0.05$) in the control groups ($p < 0.01$). In *B. bufo*, maximum body mass was 0.35 g in control groups and 0.30 g in mixed groups; at metamorphosis the respective body masses were 0.20 g and 0.19 g. In *B. viridis*, however, body mass increased until stage 42 to 0.97 g (control) and 0.91 (mixed), with differences between control and mixed groups being significantly higher at only some mixed group treatments (Kruskal-Wallis ANOVA). In *B. viridis*, body mass at metamorphosis was 0.64 g (control) and 0.65 g (mixed). Body condition indices are shown in Fig. 5. The marked decrease in body condition indicates that tadpoles lose much of their weight during metamorphic climax when feeding stops. Differences in body condition were higher in *B. bufo*, with individuals of the control groups being in better condition except at stage 43. The differences were significant ($p < 0.05$) except at stage 36, 38, 39 and 42. In *B. viridis* tadpoles, differences in body condition were smaller, with mixed-group larvae being in better condition (differences were only significant for stage 43 and 45; $p < 0.05$).

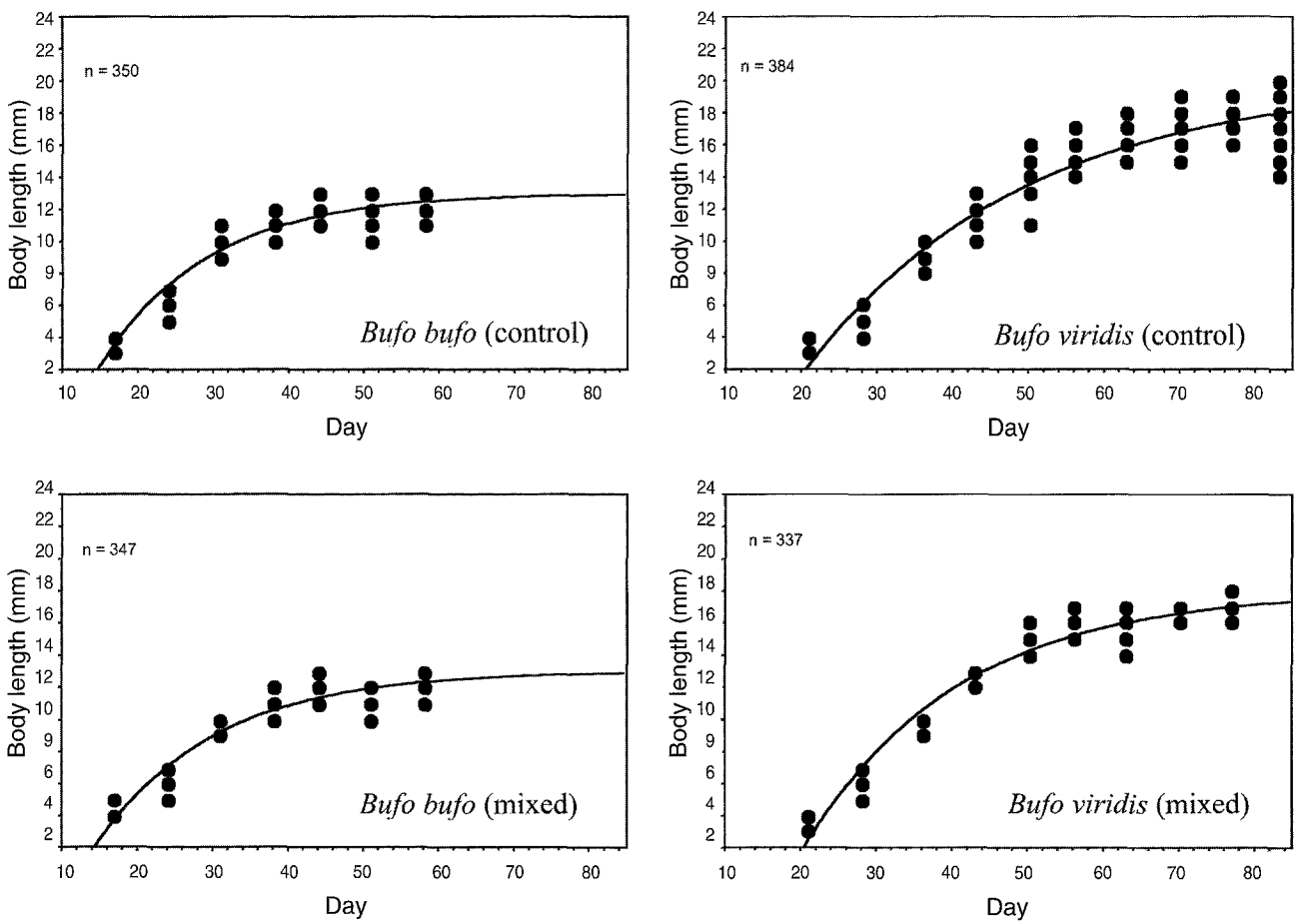

Fig. 3. Relationship between time (days) and body length (mm) of larvae of *B. bufo* and *B. viridis* in control and mixed groups. Day 1 = hatching day (04 Apr 2001 for *B. bufo* and 12 Apr 2001 for *B. viridis*). Regression parameters are given in Table 2. Due to overlapping, each dot may represent numerous tadpoles.

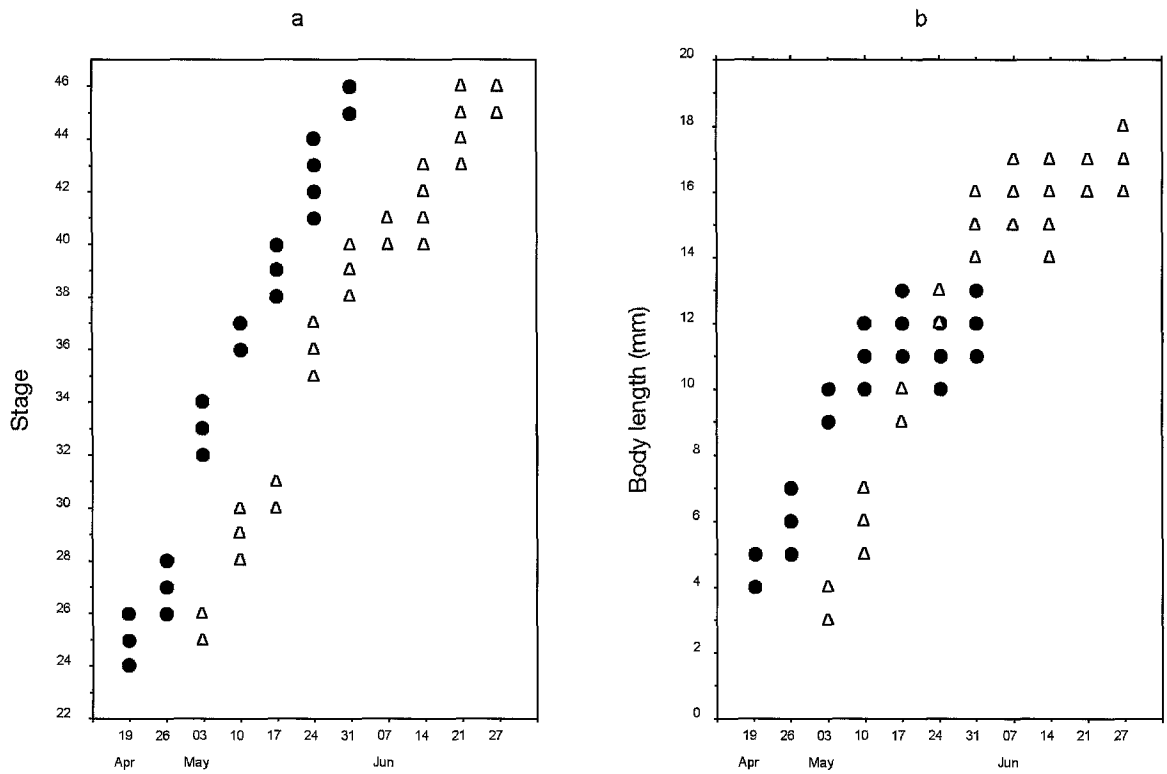

Fig. 4. Date and (**a**) larval developmental stages after GOSNER (1960) and (**b**) body length (mm) of *B. bufo* (●) and *B. viridis* (△) co-occurring during mixed group treatments. Due to overlapping, each dot may represent numerous tadpoles.

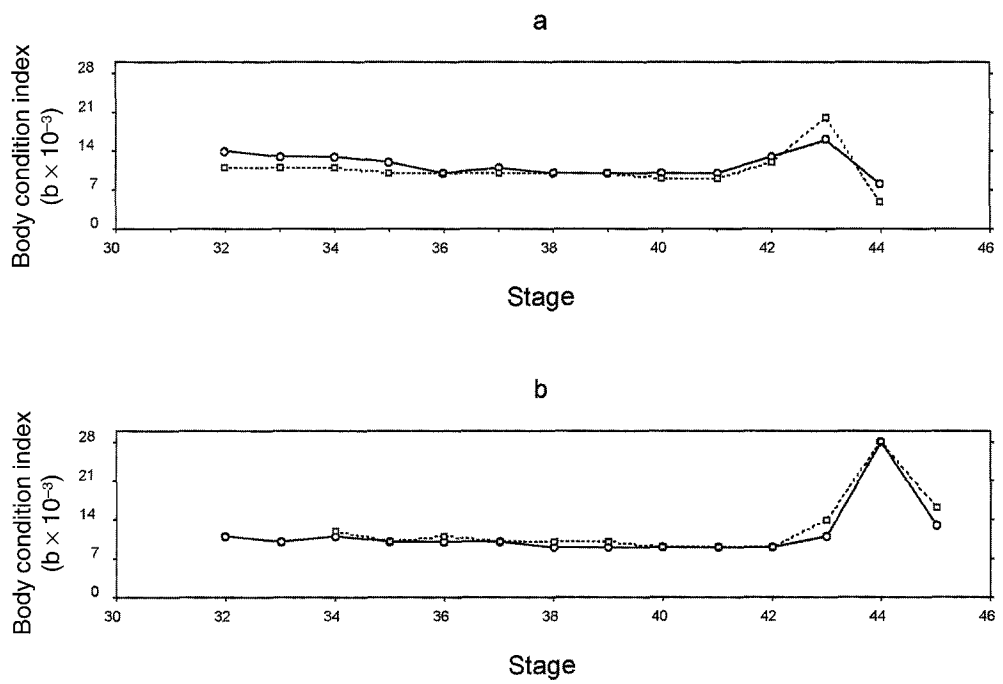

Fig. 5. Body condition index during larval development of *B. bufo* (**a**) and *B. viridis* (**b**) in control (–○–) and mixed groups (--□--). Stages after GOSNER (1960).

Table 3. Summary of laboratory experiment data for *B. bufo* and *B. viridis* in control and mixed groups. $^{n.s}$ not significant ($p > 0.05$); * significant ($p < 0.05$); ** highly significant ($p < 0.01$); *** very highly significant ($p < 0.001$).

	Bufo bufo		*Bufo viridis*	
	control	mixed	control	mixed
Length of larval period	same$^{n.s.}$	same$^{n.s.}$	longer***	shorter***
Differentiation rate	lower$^{n.s.}$	higher$^{n.s.}$	lower***	higher***
Growth rate	higher$^{n.s.}$	lower$^{n.s.}$	higher**	lower**
Tail length	longer*	shorter*	longer*	shorter*
Body mass	higher**	lower**	partly lower**	partly higher**
Body condition index	higher*	lower*	partly lower*	partly higher*
Body condition index at metamorphosis	higher*	lower*	lower*	higher*
Mass at metamorphosis	higher$^{n.s}$	lower$^{n.s.}$	lower$^{n.s.}$	higher$^{n.s}$
Size at metamorphosis	higher$^{n.s}$	lower $^{n.s}$	higher**	lower**
Survival rate	lower*	higher*	lower$^{n.s}$	higher$^{n.s}$

Metamorphosis

For *B. bufo* no significant differences between treatments were found with respect to body size and body mass at metamorphosis, whereas toadlets of *B. viridis* were significantly larger in control groups ($p < 0.05$), but without significant differences ($p > 0.05$) in body mass. Survival rates were very high in both monospecific (86–89%) and in mixed groups (92–97%), but for both species higher in mixed groups.

Discussion

Our experiments clearly show statistically significant differences in the duration of larval period, growth, body mass and body condition index when comparing mixed *versus* single-species groups (Table 3). As also described by SMITH-GILL & BERVEN (1979) and TEJEDO & REQUES (1994a, b) the developmental rate was linear in both species at all treatments. In *B. bufo* no effect of competition on the duration of the larval period was detected, whereas in *B. viridis* it was highly significantly shorter in the mixed-species design (mixed: 77 days, control: 83 days). In natural ponds it is a distinct ecological advantage to leave the water as early as possible in order to escape the high predation pressure and the ever increasing desiccation risk in the summer season (WASSERSUG 1975); however, a shorter larval period often means smaller toadlets at metamorphosis (WILBUR & COLLINS 1973; SMITH-GILL & BERVEN 1979).

Amphibian larval growth is rather variable, depending on several factors such as temperature, pH, hydroperiod, predation pressure, quality and quantity of food supply (e.g. SMITH-GILL & BERVEN 1979; NEWMAN 1992; KUPFERBERG et al. 1994; TEJEDO & REQUES 1994a, b) and competition (GRIFFITHS 1991). In species breeding in temporal water bodies, the size spread is even larger (WILBUR & COLLINS 1973).

In our experiments, growth curves were asymptotic in both species, stagnating in developmental stage 38/39 (GOSNER 1960), at the start of prometamorphosis, as also described by other authors (e.g. TEJEDO & REQUES 1994a, b). Larvae of *B. viridis* showed higher growth rates in control groups. Green toadlets from mixed groups were smaller (16.9 mm *versus* 17.6 mm in control groups), probably due to their faster development (see above). Nevertheless, even the smallest larvae from the laboratory within a given developmental stage were equal or bigger in length when compared with animals in the field (KATZMANN 2002; NÖLLERT & NÖLLERT 1992). No significant negative effects of competition on *B. bufo* were observed. GOLLMANN & GOLLMANN (1993) obtained similiar results in a competition experiment using tadpoles of two Australian species: The bigger tadpoles reached metamorphosis earlier and at a larger body size in mixed groups. In the present study *B. viridis* also entered metamorphosis earlier, but at a smaller body size than the control group.

In all developmental stages, mixed-group larvae of the common toad weighed significantly less than those of the control group, whereas in the larvae of the green toad the opposite was true. In other studies species also reached a lower body mass at metamorphosis in mixed groups (MORIN 1983; KUPFERBERG 1997; GRIFFITHS et al. 1993; LAURILA 2000). In our experiments, species-specific differences in body size and foraging behaviour might have caused these deviations in the weight increment of the two species (see also MORIN & JOHNSON 1988); since the *B. viridis* larvae are bigger than those of *B. bufo* and possess a wider mouth opening, they probably can feed more efficiently than their competitors. We observed that *B. viridis* tadpoles grazed on the water surface, whereas *B. bufo* larvae often fed in deeper water layers. We fed a mixture of fish food and nettle powder, which initially floated on the water surface before sinking to the bottom

of the tanks. Thus, most of the protein-rich fish fodder was probably taken by the stronger *B. viridis* larvae before reaching the feeding grounds of *B. bufo*. In contrast to the findings of other authors that bigger tadpoles actively hindered smaller ones in feeding (WILBUR 1977), our experiments revealed no such active interactions.

B. viridis toadlets, which reached a higher body condition index in a shorter larval period in mixed groups, although being smaller, profited by the decrease of intraspecific competitive stress when compared with their conspecifics from the control groups. They had access to more high-quality, protein-rich food. Better nutritional conditions not only guarantee a good physical condition but also shorten the larval period (e.g. KUPFERBERG et al. 1994). Moreover, *B. viridis* larvae (from GOSNER stage 39 onwards) might have taken advantage from the release of competition stress since *B. bufo* entered metamorphosis earlier. Especially in temporary pond breeders such as *B. viridis*, which risk a high mortality by desiccation, faster developmental rates would be highly adaptive despite being detrimental to metamorphic size. This is consistent with the results of TEJEDO & REQUES (1994b), who found that *B. calamita* larvae accelerated their development rather than increased their metamorphic size when shifted to a higher food resource level. Other studies revealed that competitive ability is often influenced by foraging activity more than by body size (MORIN & JOHNSON 1988; LAURILA 2000).

Our experiments indicate high intraspecific competition in *B. viridis*, whereas *B. bufo* suffered from interspecific competition in mixed groups, resulting in a lower body condition index and a decrease in weight (Table 3). These results are in accordance with other authors who observed that bigger larvae are superior to smaller ones (GRIFFITHS 1991; GOLLMANN & GOLLMANN 1993) and that temporary pond larvae are superior to permanent pond larvae (WILBUR 1987). In natural habitats these competitive effects are often concealed by abiotic factors such as pond hydroperiod (TEJEDO & REQUES 1994a; DENVER 1997; LOMAN 1999) and predation pressure (MORIN 1983; BARDSLEY & BEEBEE 1998a; VAN BUSKIRK & MC COLLUM 1999). As *B. bufo* larvae are unpalatable to vertebrate predators (HEUSSER 1971), they can cope better with the high predator density in permanent ponds (CLAUSNITZER 1983). Insect predators, which frequently forage *B. bufo* larvae (CHOVANEC 1992), are kept at low densities by fish populations in permanent ponds. Therefore, under the environmental conditions of their usual breeding sites, their competitive inferiority will be balanced by advantages in managing predation pressure and the stable water regime of their habitat. In stark contrast, temporary pond dwellers suffer a high desiccation risk and are exposed to highly varying temperature regimes. This illustrates that the outcome of competition under natural conditions will be strongly influenced by the habitat type (BARDSLEY & BEEBEE 1998a, b; LAURILA 2000). In England (BANKS & BEEBEE 1987), temporal pond species such as *B. calamita* are inferior to *B. bufo* when breeding in permanent ponds. Moreover, spatial and temporal niche differentiation, as well as differences in feeding ecology, can faciliate competition in natural ponds (HEYER 1973; LÖSCHENKOHL 1986). This is supported by the findings of SINSCH et al. (1999), who observed no competitive effects in a syntopic population of *B. bufo, B. calamita* and *B. viridis* in German gravel pit habitats because the three species inhabited different microhabitats.

Acknowledgements

We wish to thank Michael Stachowitsch for correcting the English text.

References

BAKER, G. C. & BEEBEE, T. J. (1997): Microenvironmental effects on competition between *Rana* and *Bufo* larvae, and on the abundance of *Prototheca richardsi*, in small fish ponds. Herpetological Journal **7**: 149–154.

BANKS, G. & BEEBEE, T. J. C. (1987): Spawn predation and larval growth inhibition as mechanisms for niche seperation in anurans. Oecologia **72**: 569–573.

BARDSLEY, L. & BEEBEE, T. J. (1998a): Interspecific competition between larvae is not an important structuring force in mixed communities of *Rana* and *Bufo* on an English sand-dune system. Ecography **21**: 449–456.

BARDSLEY, L. & BEEBEE, T. J. (1998b): Interspecific competition between *Bufo* larvae under conditions of community transition. Ecology **79**: 1751–1759.

BEEBEE, T. J. C. (1995): Tadpole growth: is there an interference effect in nature? Herpetological Journal **5**: 204–205.

CABELA, A., GRILLITSCH, H. & TIEDEMANN, F. (2001): Atlas zur Verbreitung und Ökologie der Amphibien und Reptilien Österreichs. Hrsg. Umweltbundesamt Wien.

CHOVANEC, A. (1992): The influence of tadpole swimming behaviour on predation by dragonfly nymphs. Amphibia-Reptilia **13**: 341–349.

CLAUSNITZER, H. J. (1983): Zum gemeinsamen Vorkommen von Amphibien und Fischen. Salamandra **19**: 158–162.

DENVER, R. J. (1997): Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. American Zoologist **37**: 170–184.

EIBL-EIBESFELDT, I. (1953): Bestimmung der Kaulquappen nach ihrem Verhalten. Die Aquarien- und Terrarienzeitschrift (Stuttgart) **6**: 16–18.

GOLLMANN, G. & GOLLMANN, B. (1993): A laboratory experiment on interspecific competition between tadpoles of *Geocrinia victoriana* and *Pseudophryne semimarmorata* (Anura, Myobatrachinae). Amphibia – Reptilia **14**: 349–356.

GOSNER, K. L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**: 183–190.

GRIFFITHS, R. A. (1991): Competition between common frog, *Rana temporaria,* and natterjack toad, *Bufo calamita,* tad-

poles: the effect of competitor density and interaction level on tadpole development. Oikos **61**: 187–196.

GRIFFITHS, R. A., DENTON, J. & WONG, A. L. (1993): The effect of food level on competition of tadpoles. Journal of Animal Ecology **62**: 274–279.

GRIFFITHS, R. A. & FOSTER, J. P. (1998): The effect of social interactions on tadpole activity and growth in the British anuran amphibians (*Bufo bufo, B. calamita, Rana temporaria*). Journal of Zoology (London) **245**: 431–437.

HEMMER, H. & KADEL, K. (1970): Zur Laichplatzauswahl der Kreuzkröte (*Bufo calamita*) und der Wechselkröte (*Bufo viridis*). Aquaterra **7**: 123–127.

HEMMER, H. & BOEHME, W. (1974): Nachweis natürlicher Bastardisierung der Erdkröte (*Bufo b. bufo)* und der Wechselkröte (*Bufo v. viridis*) im Rheinland. Salamandra **10**: 126–130.

HEUSSER, H. (1971): Differenziertes Kaulquappen-Fressen durch Molche. Experientia **27**: 475.

HEYER, R. W. (1973): Ecological interactions of frog larvae at a seasonal tropical location in Thailand. J. Herpetol. **7**: 337–362.

KATZMANN, S. (2002): Das Larvenwachstum von Erdkröte (*Bufo bufo*) und Wechselkröte (*Bufo viridis*) in isolierten und syntopen Vorkommen. Diploma Thesis, University of Vienna.

KIESECKER, J. & BLAUSTEIN, A. R. (1999): Pathogen reverses competition between larval amphibians. Ecology **80**: 2442–2448.

KUPFERBERG, S. J. (1997): The role of larval diet in anuran metamorphosis. American Zoologist **37**: 146–159.

KUPFERBERG, S. J., MARKS, J. C. & POWER, M. E (1994): Effects of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life-history traits. Copeia **1994**: 446–457.

LAURILA, A. (1998): Breeding habitat selection and larval performance of two anurans in freshwater rock-pools. Ecography **21**: 484–494.

LAURILA, A. (2000): Competitive ability and the coexistence of anuran larvae in freshwater rock-pools. Freshwater Biology **43**: 161–174.

LOMAN, J. (1999): Early metamorphosis in common frog *Rana temporaria* tadpoles at risk of drying: an experimental demonstration. Amphibia – Reptilia **20**: 421–430.

LÖSCHENKOHL, A. (1986): Niche partitioning and competition in tadpoles. In: Z. ROCEK (ed.), Studies in Herpetology, pp. 399–402. Prague.

MERILÄ, J., LAURILA, A., PAHKALA, M., RÄSÄNEN, K. & TIMENES LAUGEN, A. (2000): Adaptive phenotypic plasticity in timing of metamorphosis in the common frog *Rana temporaria.* Ecoscience **7**: 18–24.

MORIN, P. J. (1983): Predation, competition, and the composition of larval anuran guilds. Ecological Monographs **53**: 119–138.

MORIN, P. J. & JOHNSON, E. A. (1988): Experimental studies of asymmetric competition among anurans. Oikos **53**: 398–407.

NEWMAN, R. A. (1992): Adaptive plasticity in amphibian metamorphosis. Bioscience **42**: 671–678.

NÖLLERT, A. & NÖLLERT, C. (1992): Die Amphibien Europas. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart.

PEACOR, S. D. & WERNER, E. E. (1997): Trait mediated indirect interactions in a simple aquatic food web. Ecology **78**: 1146–1156.

PETRANKA, J. W. (1995): Interference competition in tadpoles: Are multiple agents involved ? Herpetological Journal **5**: 206–207.

SINSCH, U., HÖFER, S. & KELTSCH, M. (1999): Syntope Habitatnutzung von *Bufo calamita, B. viridis* und *B. bufo* in einem rheinischen Auskiesungsgebiet. Zeitschrift für Feldherpetologie (Bochum) **6**: 43–64.

SMITH-GILL, S.J. & BERVEN, K. A. (1979): Predicting amphibian metamorphosis. American Naturalist **113 (4)**: 563–585.

STATSOFT (1999): Statistica for Windows version 5.5. Tulsa, USA.

TEJEDO, M. & REQUES, R. (1994a): Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. Oikos **71**: 295–304.

TEJEDO, M. & REQUES, R. (1994b): Does larval growth history determine the timing of metamorphosis in anurans; a field experiment. Herpetologica **50**: 113–118.

TRAVIS, J. (1980): Phenotypic variation and the outcome of interspecific competition in hylid tadpoles. Evolution **34**: 40–50.

VAN BUSKIRK, J. & MCCOLLUM, S. (1999): Plasticity and selection explain variation in tadpole phenotype between ponds with different predator composition. Oikos **85**: 31–39.

VIERTEL, B. (1981): Wachstumsraten, Gewichtszustandswert und Ätilität bei Erdkrötenlarven (*Bufo bufo* L.) im Freiland. Salamandra (Frankfurt/ M.) **17**: 20–42.

WASSERSUG, R. J. (1975): The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. American Zoologist **15**: 405–417.

WELLBORN, G. A., SKELLY, D. K. & WERNER, E. E. (1996): Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics **27**: 337–363.

WERNER, E. (1994): Ontogenetic scaling of competitive relations: size dependent effects and responses in two anuran larvae. Ecology **75**: 197–213.

WERNER, E. & ANHOLT, B. (1996): Predator-induced behavioural indirect effects: consequences to competitive interactions in anuran larvae. Ecology **77**: 157–169.

WILBUR, H. M. & COLLINS, J. P. (1973): Ecological aspects of amphibian metamorphosis. Science **182**: 1305–1314.

WILBUR, H. M. (1977): Density dependent aspects of growth and metamorphosis in *Bufo americanus.* Ecology **58**: 196–200.

WILBUR, H. M. (1987): Regulation of structure in complex systems: experimental temporary pond communities. Ecology **68**: 1437–1452.

WONG, A. L., GRIFFITHS, R. A. & BEEBEE, T. J. C. (2000): The influence of tadpole size on cell – mediated competition between larvae (*Bufo calamita* and *Rana temporaria*) in the laboratory. Amphibia – Reptilia **21**: 431–438.

WOODWARD, B. D. (1982): Tadpole competition in a desert anuran community. Oecologia **54**: 96–100.

WOODWARD, B. D. (1983): Predator-prey interactions and breeding pond use of temporary-pond species in a desert anuran community. Ecology **64**: 1549–1555.

ZAR, J. H. (1984): Biostatistical analysis. Department of Biological Sciences, Northern Illinois University.